VARIATIONS OF TEMPERATURE IN MALE CONES OF ENCEPHALARTOS ALTENSTEINII LEHM.

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A fact which has been known to the writer since early childhood is that the male cones of at least one species of *Encephalartos* show a considerable rise in temperature during the period of pollen shedding. It is not now possible to say with certainty which species supplied the evidence, but the plant was probably one growing in or near Durban, and may have been in the Botanic Gardens there. Knowing that the cones become heated during the liberation of pollen, it was somewhat of a disappointment to find, on going through the literature available, only one reference to this phenomenon, a brief remark in *Les Gymnospermes actuelles et fossiles*, by H. Gaussen. This remark is to the effect that the cones have a feverish temperature, and there is no indication as to where the information had been obtained.[1] Other works ignore the matter entirely.

Male cones were cut off two plants of *Encephalartos altensteinii* Lehm., for use in the practical classes for students in the second and third year botany courses at Rhodes University, Grahamstown, during April, 1958, and observations made of the temperature changes. This was done at first merely as a possible demonstration of the rise, known to the writer to occur, and to show how great it is—most aptly described by Gaussen, in the work already referred to, as "le cône présente une veritable fièvre". It was, as was later found out, a most fortunate chance that *E. altensteinii* was chosen, as, of the species available, it was the most suitable. When discussion with various workers whose knowledge of *Encephalartos* and allied genera greatly exceeds that of the writer, showed that apparently no one had much, if any, idea of this temperature rise, observations were made on a number of cut-off cones of *E. altensteinii* in the laboratory and cones *in situ* on plants in the Botanic Gardens of Grahamstown, where the first lot of cones had come from. It was not practicable to carry out full-scale observations out of doors with the delicate thermometers being used, but better methods of measuring the internal temperatures of plants are available by other means and it is hoped to employ these later.

Ordinary glass laboratory thermometers registering up to 100 degrees C. were used: these were inserted between the sporophylls of the cones at various positions from base to tip and a control thermometer was placed next to the cones, neither touching them nor close enough to be materially affected by any radiated heat, but registering the air temperature in the vicinity of the cones. The expected rise in temperature was duly observed, and it was then noticed that it apparently follows a diurnal rhythm, a fact not mentioned by Gaussen, and one which also may serve to explain in part why the temperature rise has been overlooked by most workers. There is also a possibility that there is a strong connection between the temperature rise and the actual shedding of pollen: it would seem that pollen is shed very freely during the afternoon hours, when the temperature of the cones is at the highest level (see tables), but if as much as possible of the pollen is shaken off at about six o'clock in the evening, apparently only a little is shed from then until after noon on the following day. It is also possible that what does seem to be shed then is only what was trapped the day before and released owing to movements of the sporophylls or of the various insects which infest the cones. (At least three species of weevils were common in the male cones of *E. altensteinii* used, and a tenebrionid beetle was found in great numbers in most of the cones. The dimorphic weevil, *Antliarrhinus zamiae* Thunb. (*Antliarrhinus rectirostris* Gyl.) was common on female cones of *E. horridus* Lehm. only, at the time when a gelatinous exudate appeared: otherwise, very few of this type of weevil were seen.)

The temperature of a cone is not the same over all its length; the greatest rise and hence the greatest difference between cone temperature and air temperature occurs, as far as has been observed, about the middle third of the cone, and it would seem that there may be a gradual progression of the maximum temperature zone further up the cone, towards the apex, during the course of pollen shedding. The observations made have been of a preliminary nature and on cones already fairly far advanced in growth at the pollen shedding stage, but the tables given below show clearly the diurnal rhythm and the position of greatest temperature rise. The greatest difference noted for any cone at any time, as compared with air temperature, was one of 17 degrees C. in the laboratory, the cone having been cut from the parent plant four days before. In the open, with the cones still attached to the parent plant, the difference, on a windy day, was on one occasion 10 degrees C.

The male cones of *E. Lehmannii* Lehm. were also tested but though in the field they appeared to show a difference between parts of the cone and the surrounding air, as tested roughly by feeling with the hand, the results from these cones in the laboratory do not produce the striking differences that are obtained with the cones of *E. altensteinii.* The rise is often so great in the latter that, compared with the air in the afternoon hours, the cone feels hot to the hand, and it is also possible to distinguish with ease which area is warmest, over a period of several days in the laboratory.

The plants from which the first supply of *E. altensteinii* cones were obtained are a clump of six, one of which has a trunk about 10 feet tall, the rest being grouped round its base and being almost stemless. The large plant bore four cones and the smaller plants three, three, two, one and no cones, respectively. The cones were ripe at various dates from late March into early May and at the beginning of July two had not yet entirely lost their yellow and green colouring, but showed no temperature rise. They averaged 17 inches in length, including the peduncle, but later cones obtained through the kindness of Mrs. J. Rennie, from other *Encephalartos* plants growing elsewhere in Grahamstown, averaged 24 inches. These cones appeared to be of the *E. altensteinii* type and the description given of the plants fitted *E. altensteinii* also, so that the cones were considered of this species in the tests.

Of the great number of *Encephalartos* plants growing in Grahamstown, only two groups are known to the writer to have borne female cones during the first half of 1958. Male cones were produced by perhaps twenty plants and the rest showed no signs of cone production whatever.[2] The female cones belonged to *E. altensteinii* and *E. horridus* Lehm. There does not seem to be anything approaching the same temperature rise and fall in the female cones, as in the male cones of *E. altensteinii*, but testing of the female cones is not possible with ordinary thermometers without damaging the cones.

All the cones tested, of *E. altensteinii* and *E. villosus* Lehm., had a peculiar and distinctive, strong, but not particularly unpleasant, smell; those of *E. lehmannii*, however, had no apparent odour. This is contrary to the experience of Miss Pegler[3] with the cones of *E. villosus* in the open. During the tests of the cones of *E. villosus*, negative results were obtained for temperature rise, as was to be expected, owing to the extremely loose, open construction of the cone and the simple methods used for taking the temperatures.

REFERENCES.

(1) GAUSSEN, H. (1944): Les Gymnospermes actuelles et fossiles. Fasc. II, Chap. III (p. 43): Toulouse, Faculté des sciences.

(2) HENDERSON, M. R. (1945): Materials for a Revision of the South African Species of Encephalartos. *Jour. S.A. Bot.*, Vol. XI.

(3) PEARSON, H. H. W. (1906): Notes on South African Cycads—I. *Trans. S.A. Phil. Soc.*, Vol. XVI, Part 4, pp. 341–354.

(4) LEICK, E. (1910): Untersuchungen über die Blütenwärme der Araceen. Griefswald. p. 9. ,, . . . die überraschend hohen Temperaturen der Araceen blütenstände, sowie ihre eigenartigen Wärmeschwankungen, die höchstens noch in dem Verhalten der Cycadeen-infloreszenzen und der Victoria regia." Further, p. 56. ,,Es muss aber betont werden, dass Temperaturüberschusse von gleicher Höhe wie bei den Araceen nur bei einigen Cycadeen Palmen und bei Victoria regia ermittelt werden."

(5) LEICK, E. (1915): Berichte der deutschen botanischen Gesellschaft. Band XXXIII. p. 519: Leick states that Cycads, Palms and Victoria regia ,,ähnlich hohe Eigenwärmegrade gemessen wurden wie bei den Araceen."

(6) HUBER, B. (1935): Der Wärmehaushalt der Pflanzen. *F. Boas, Munchen*, Naturwissenschaft und Landwirtschaft. Verlag Dr. F. P. Datterer & Cie., Freising-Munchen.
p. 89. ,,Es wird angegeben: für Cycadeen (Kraus 1896): wochenlang anhaltende tagesperiodische Selbsterwärmung der männlichen Blütenzapfen bis zu 13° Ubertemperatur; der Zeitpunkt des Tagesmaximums verschiebt sich im verlauf der Blüte gesetzmässig, ebenso verschiebt sich der Zeitpunkt des Maximums von der Spitze (früher) gegen die Basis (später);"
p. 90. ,,Bei den grossenteils windblütigen Cycadeen (über ihre Käferblütigkeit vgl. Diels 1916) und Palmen wird die Erwärmung erst recht eine blosse Begleiterscheinung der raschen Stoffmobilisierung sein, die sich auch im Verschwinden der Stärkeworräte des Stammes und der Entwicklung hoher lokaler Blutungsdrucke äussert."

TABLE I.

Encephalartos altensteinii: male cone, collected 12.4.1958 and left lying on laboratory bench. Large amount of pollen being shed.

Date.	Time.	Temperature, in degrees C.	
		Air.	Cone 1.
14.4.1958	11.30 a.m.	20·0	22·0
	3.0 p.m.	21·0	36·0
	3.30 p.m.	21·0	36·0
	4.30 p.m.	20·0	37·0
15.4.1958	11.0 a.m.	20·0	20·0
	12.30 p.m.	21·0	21·0
	2.15 p.m.	21·0	24·0
	3.0 p.m.	21·0	26·5
	3.30 p.m.	20·5	30·0
	4.50 p.m.	20·5	35·0
	6.10 p.m.	20·0	37·0

TABLE II.

Encephalartos altensteinii: male cones.

Date.	Time.	Temperature, in degrees C.				
		Air.	Cone 2.	Cone 3.		
				Lower.	Middle.	Upper.
16.4.58	8.45 a.m.	—	17·0	—	—	—
	9.30 a.m.	16·0	—	17·0	18·5	18·5*
	10.30 a.m.	17·0	18·0	17·0	18·5	17·0
	11.30 a.m.	18·0	—	18·0	19·0	18·0
	12.10 p.m.	19·0	18·7	18·0	19·0	18·2
	1.0 p.m.	19·5	20·0	19·0	20·0	19·0
	2.10 p.m.	19·6	23·0	20·0	22·0	20·3
	2.23 p.m.	20·0	23·5	20·5	23·0	20·5
	3.15 p.m.	20·0	27·0	22·0	26·0	22·0
	3.32 p.m.	20·4	28·0	22·0	27·0	22·2
	3.45 p.m.	20·4	29·0	22·5	27·8	22·6
	3.57 p.m.	20·3	30·0	22·9	28·3	22·8
	4.10 p.m.	20·0	31·0	23·0	28·5	22·8
	4.40 p.m.	20·0	33·4	23·8	30·0	23·5
17.4.58	9.0 a.m.	18·5	19·0	17·5	18·0	18·2
	10.30 a.m.	19·5	19·0	18·5	19·0	19·0
	11.0 a.m.	19·8	19·8	18·8	19·2	19·2
	11.25 a.m.	20·2	20·2	19·2	19·5	20·0
	12.35 p.m.	21·5	22·8	21·5	21·5	22·2
	1.55 p.m.	22·4	28·0	24·6	26·2	25·5
	4.30 p.m.	22·5	36·8*	28·0	34·5	30·5
	5.40 p.m.	21·5	36·5	29·0	34·0	30·0
	6.0 p.m.	21·2	37·0	28·8	34·0	29·8
18.4.58	6.0 p.m.	22·4	35·0	26·5	30·4	26·4
19.4.58	5.40 p.m.	23·0	33·0	24·5	26·0	24·5
21.4.58	5.0 p.m.	23·0	25·8	23·0	23·4	23·0
22.4.58	5.0 p.m.	20·5	22·0	21·0	21·0	21·0

Hereafter the temperatures were not significantly different.

* Indicates the reading is higher than the following one, during rising temperatures.

TABLE III.

Encephalartos altensteinii: new male cones, collected 22.4.58.

Date.	Time.	Temperature, in degrees C.									
		Air.	Cone 4.			Cone 5.			Cone 6.		
			Lower.	Middle.	Upper.	Lower.	Middle.	Upper.	Lower.	Middle.	Upper.
22.4.58	5.0 p.m.	20·5	26·0	28·5	25·8	27·5	29·0	26·3	27·8	28·0	23·0
23.4.58	9.0 a.m.	20·0	21·0*	21·0	21·0	21·2	21·2	20·8	21·2	21·2	20·4
	11.45 a.m.	20·5	20·0	21·4	21·2	21·5	21·6	21·2	21·5	21·5	21·0
	2.0 p.m.	20·5	23·2	24·2	23·2	24·4	25·0	24·0	25·0	25·2	23·0
	4.0 p.m.	20·0	24·0	26·2	24·2	25·4	27·8	25·4	27·2	27·8	23·0
	4.45 p.m.	20·0	24·0	26·5	23·8	25·2	28·0	25·0	27·4	28·0	22·4
24.4.58	9.15 a.m.	19·6	20·0	20·4	20·0	20·4*	20·5	20·4	20·2	20·0	20·0
	11.15 a.m.	20·2	20·5	21·0	20·8	20·0	21·4	20·8	21·2	21·0	20·8
	4.15 p.m.	22·0	24·8	26·8	25·6	26·8	31·0	27·0	29·8	30·5	25·5
	5.30 p.m.	21·6	25·0	27·2	25·5	26·4	31·6	27·2	30·5	31·5	25·2
25.4.58	2.0 p.m.	22·4	23·4	24·0	24·0	24·8	25·4	24·4	25·0	25·0	24·0
	4.0 p.m.	22·0	24·4	25·5	24·8	25·2	27·5	26·0	27·2	27·2	25·4
26.4.58	Noon	20·5	21·0	21·5	21·0	21·5	21·5	21·8	22·0	22·5	22·5
28.4.58	Noon	21·2	20·5	21·2	21·5	21·5	21·0	21·8			
29.4.58	11.30 a.m.	16·0	15·0	15·5	15·4	16·2	16·2	16·0	Removed for other purposes.		
	12.45 p.m.	18·6	16·0	16·5	16·5	17·0	16·8	17·0			
	2.15 p.m.	18·8	17·0	17·4	17·2	18·0	17·5	18·0			
	4.40 p.m.	18·5	17·5	18·2	18·0	18·5	18·4	18·4			

TABLE IV.

Encephalartos lehmannii: male cones.

Date.	Time.	Temperature, in degrees C.						
		Air.	Cone 1.			Cone 2.		
			Lower.	Middle.	Upper.	Lower.	Middle.	Upper.
3.5.58 ..	10.0 a.m.	18·4	18·0	18·0	18·0	18·0	18·0	18·4
	5.30 p.m.	18·0	18·0	18·0	18·0	18·0	18·0	18·5
5.5.58 ..	5.45 p.m.	15·0	15·8	16·0	16·0	15·4	15·6	16·0
6.5.58 ..	5.0 p.m.	18·0	18·5	19·0	19·0	18·0	18·0	19·0
7.5.58 ..	2.0 p.m.	19·8	19·8	20·2	20·8	—	—	20·6
9.5.58 ..	2.0 p.m.	19·4	20·0	20·2	20·0			
	4.0 p.m.	19·5	20·0	21·4	20·2			
	5.0 p.m.	19·0	20·0	20·5	20·0			
	5.45 p.m.	18·5	19·5	20·0	19·8			

TABLE V.

Encephalartos altensteinii and *Encephalartos villosus*: male cones.

Date.	Time.	Temperature, in degrees C.						
		Air.	*E. altensteinii.*			*E. villosus.*		
			Lower.	Middle 1.	Middle 2.	Upper.	Lower.	Middle.
9.5.58 ..	2.0 p.m.	19·4	26·0	—	24·2	24·0	—	—
	4.0 p.m.	19·5	30·5	31·5	28·5	28·0	18·5	18·0
	5.0 p.m.	19·0	29·8	31·0	28·0	27·5	18·0	18·0
	5.45 p.m.	18·5	27·5	29·5	26·0	25·5	17·5	17·0

TABLE VI.

Encephalartos altensteinii: male cones *in situ* on plants, Botanic Gardens.

Date.	Time.	Temperature, in degrees C.			Remarks.
		Air.	Cone.		
			Lower.	Middle.	
22.4.58 ..	3.0 p.m.	16·2	19·8	20·0	Much wind, exposed position, but in shade of building.
	3.15 p.m.	16·2	19·8	19·4*	
	3.30 p.m.	16·2	20·0	20·0	
25.4.58 ..	3.0 p.m.	19·8	22·6	23·0	Moderately still, slight breeze: plant in shade of building.
	3.30 p.m.	20·2	25·8	27·0	
	3.45 p.m.	20·2	26·8	30·2	
	4.15 p.m.	20·0	24·8	29·0	